

electron transport particles or ETP). Another fraction supported phosphorylation when oxidizing compounds other than succinate (he termed these *phosphorylating electron transport particles* or PETP). To understand the genesis of these particles, Green collaborated with electron microscopist Hans Ris.²¹ The resulting micrographs revealed open fragments of cristae in the PETP and less functional closed fragments of cristae in the ETP particles (Green, 1957–8; Ziegler et al., 1958). This supported Palade's suggestion that the processes of oxidative phosphorylation were localized in the cristae.

Youssef Hatefi, working in Green's laboratory, developed evidence for grouping the various substances involved in the electron transport chain into four complexes:

- (I) an NADH-ubiquinone reductase complex which included FMN and non-heme iron
- (II) a succinate-ubiquinone reductase complex which included FAD and nonheme iron
- (III) a ubiquinol-cytochrome *c* reductase complex which included cytochromes *b* and *c*₁, and a nonheme iron protein; and
- (IV) a cytochrome *c* oxidase complex which included cytochrome *a* and copper.

Thereafter four of Green's collaborators, Hatefi, Haavik, Fowler, and Griffiths (1962), succeeded in reconstituting two systems: one capable of oxidizing NADH to carbon dioxide and water by combining complexes I, III, and IV, and another capable of oxidizing succinate to carbon dioxide and water by combining complexes II, III, and IV. Both reconstitutions revealed particulate structures, suggesting that the respiratory chain was formed into a fixed assembly electron transfer system (one in which the molecules were in advantageous spatial relations for passing electrons sequentially from molecule to molecule).

²¹ Ris did his graduate work on mitotic division with Franz Schrader in zoology at Columbia. Subsequently, he spent a number of years working in Mirsky's laboratory at Rockefeller. Mirsky was a biochemist by background and Ris characterizes him as teaching Ris biochemistry while Ris provided cytological understanding of the structure of chromosomes as well as procedures for isolating them. Together they published a number of papers revealing, for example, the role of proteins in providing structure to chromosomes (Mirsky & Ris, 1951) and generating quantitative measures of DNA content in cell nuclei (Ris & Mirsky, 1949). Ris moved to the University of Wisconsin in 1949 and shortly thereafter began to explore the potential of electron microscopy for studying chromosomes, a project that did not fully bear fruit until the development of high-voltage electron microscopes in the late 1960s. Ris found Green's lack of sensitivity to cytological structure frustrating and soon suggested that Green work instead with Fernández-Morán at the University of Chicago (Interview, 6 November 1987, Madison).